

EFFECT OF FOREST STRUCTURE ON AMERICAN REDSTART FORAGING BEHAVIOR

GEORGE E. SEIDEL AND ROBERT C. WHITMORE

American Redstarts (*Setophaga ruticilla*) have been suggested to be an ecologically plastic species (Ficken 1962) which should therefore be able to adapt to a wide variety of habitat types. Removal of timber leads to a variety of forest structures which affect redstart foraging behavior. This study is an attempt to quantify foraging changes in redstarts in response to vegetation structure changes caused by different timber management practices. If changes are noted we also hope to determine specifically which habitat variables affect them.

STUDY AREAS AND METHODS

Fieldwork was conducted in the Fernow Experimental Forest, Tucker Co., West Virginia. The area was cleared of merchantable timber between 1903 and 1911. The United States Forest Service purchased the land in 1915, and in 1916 placed the area under the protection of a Forest Service Unit. In 1934, 1460 ha in the Elk Lick Run drainage was set aside as the Fernow Experimental Forest (Trimble 1977).

Hardwood tree species dominate in this forest. Oaks (*Quercus* sp.) form the most common species group, with northern red oak (*Q. rubra*) the most common species. Other common oaks include chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), and black oak (*Q. velutina*). Sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), and basswood (*Tilia americana*) are numerous on most sites. Less common species include yellow birch (*Betula lutea*), sweet birch (*B. lenta*), cucumber magnolia (*Magnolia acuminata*), butternut (*Juglans cinerea*), black walnut (*J. nigra*), American elm (*Ulmus americana*), red maple (*A. rubrum*), black locust (*Robinia pseudoacacia*), black gum (*Nyssa sylvatica*), sassafras (*Sassafras albidum*), and sourwood (*Oxydendrum arboreum*).

Two areas, watershed 1 (WS1) (30.0 ha) and watershed 4 (WS4) (38.9 ha) were used in this study. In 1958 almost all trees over 15 cm dbh were removed from WS1, and in 1971 the area was fertilized with 257 kg of urea per ha. WS1 is relatively steep, with 75% of the area having a slope of greater than 21.8°. Timber in WS1 was in the pole stage. WS4 is relatively flat, with all slopes less than 21.8°, and has not been disturbed since 1910. The timber in WS4 is approaching a mature forest.

Singing male redstarts were located in early May 1979, and their locations were marked. Foraging was observed between 06:00 and 10:00 each day throughout the nesting period except on rainy days. The observation procedure consisted of finding a redstart in a marked location and recording data on each foraging maneuver observed. Observation was terminated when the bird was lost from sight or when the bird moved outside of an area which could be covered by a circle 11.3 m in diameter (the size of the vegetational plots to be measured later).

The following information was recorded for each foraging maneuver: (1) foraging maneuver (hawk, glean, or hover [Holmes et al. 1978]), (2) substrate where the maneuver occurred (leaf or branch), (3) substrate species group (oaks, maples, beech, birch, cherries, magnolias, and

all others), (4) branch position where the maneuver occurred (proximal to trunk, middle, distal), (5) height of the maneuver. Variables 2, 3, and 4 were recorded only for gleaners or hovers.

Vegetation was measured where foraging had been observed using circular plots in a manner similar to James and Shugart (1970). Variables calculated for each plot included: (1) canopy cover in each of five vertical zones (3.1–6.1 m, 6.1–12.2 m, 12.2–18.3 m, 18.3–24.4 m, and >24.4 m); (2) maximum canopy cover in each vertical zone (percentage of points where vegetation occurred in the given zone, but none occurred in higher zones); (3) percent openings; (4) number of trees per plot <15.2 cm dbh, 15.2–30.5 cm dbh, and >30.5 cm dbh for the species groups mentioned above; and (5) maximum canopy height.

Data were analyzed using univariate and multivariate tests. Student's *t*-test was applied to vegetation variables, using each vegetation plot as a data point. Chi-square and Student's *t*-tests were applied to foraging variables, treating each foraging observation as a data point. Stepwise discriminant analysis was applied to vegetation variables, treating each bird territory as a data point, and to foraging variables after maneuvers; substrates, substrate species group, and branch positions were converted to percent for each bird. A multivariate analysis of variance (MANOVA) was used to obtain the coefficients of the canonical axis at the step of the discriminant analysis in which the best classification occurred.

RESULTS AND DISCUSSION

Data were obtained for 10 males and four females in WS1, and for nine males and three females in WS4. More females were spotted in both watersheds. However, the less conspicuous coloration and lesser amount of physical activity of females made them more difficult to observe than males. Because data were obtained on so few females, analyses were limited to males only.

The results from the univariate tests on vegetation structure variables showed that the mean canopy cover differed between watersheds in all vertical zones except the lowest (Table 1). WS1 had significantly more canopy cover in the second and third vertical zones, while WS4 had significantly more canopy cover in the fourth and fifth zones. WS1 had significantly greater values of maximum canopy cover in the third and fourth vertical zones, while WS4 had significantly more maximum canopy cover in the fifth vertical zone (Table 1). Thus, WS4 had a higher, more open canopy structure than did WS1.

Six vegetation variables entered the stepwise discriminant model at significant ($P < 0.05$) *F*-values. The variables were, in order of entry: canopy cover in the fifth vertical zone, number of large maples, number of medium beeches, maximum canopy cover in the second vertical zone, canopy cover in the second vertical zone, and number of small oaks. At this point, all territories were classified into the proper watershed, and the difference between watersheds on the basis of vegetation was significant ($F_{6,12} = 100.28$, $P < 0.0001$).

From the coefficients provided by the MANOVA, the canonical axis was calculated. Data points from WS4 grouped higher on the canonical axis

TABLE 1
MEAN AND SD OF EACH VEGETATION VARIABLE IN EACH WATERSHED^a

Variable	WS1		WS4	
	Mean	SD	Mean	SD
% canopy cover				
3.1–6.1 m	52.67	19.41	52.71	19.11
6.1–12.2 m	66.96	21.96	54.38	17.71*
12.2–18.3 m	76.96	17.81	54.79	23.52***
18.3–24.4 m	68.04	24.81	84.17	12.04**
>24.4 m	11.79	20.74	76.88	16.14***
Canopy height (m)	24.00	2.80	32.00	3.68***
% openings	17.93	7.85	22.79	7.02*
Percent maximum canopy cover				
3.1–6.1 m	1.25	2.93	0.83	1.90
6.1–12.2 m	4.82	7.51	2.29	3.61
12.2–18.3 m	22.86	24.17	1.67	3.51***
18.3–24.4 m	56.96	29.73	17.92	14.44***
>24.4 m	11.79	20.74	76.88	16.14***
No. trees/plot <15.2 cm dbh				
Oaks	0.36	1.06	0.96	2.51
Maples	7.86	5.12	7.25	6.05
Beech	0.79	1.42	2.38	3.09*
Birches	0.36	0.87	1.04	1.97
Cherries	2.79	3.38	0.00	0.00***
Magnolias	3.07	4.74	0.21	0.59**
Others	2.43	2.90	1.08	2.00
No. trees/plot 15.2–30.5 cm dbh				
Oaks	0.14	0.45	0.38	0.71
Maples	0.75	1.00	0.04	0.20***
Beech	0.00	0.00	0.13	0.34
Birches	0.00	0.00	0.33	0.64*
Cherries	0.29	0.71	0.04	0.20
Magnolias	0.50	0.88	0.13	0.34*
Others	0.71	1.15	0.50	0.72
No. trees/plot >30.5 cm dbh				
Oaks	0.07	0.26	0.58	1.02*
Maples	0.50	0.69	0.33	0.64
Beech	0.00	0.00	0.17	0.48
Birches	0.00	0.00	0.38	0.65**
Cherries	0.07	0.26	0.13	0.45
Magnolias	0.11	0.31	0.17	0.38
Others	0.11	0.31	0.29	0.55

^a Statistical significance as determined by Student's *t*-test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. WS1: $N = 28$; WS4: $N = 24$.

TABLE 2
CORRELATIONS BETWEEN CANONICAL AXIS FOR VEGETATION AND EACH OF THE SIX ORIGINAL VARIABLES, AND PROBABILITY OF A GREATER CORRELATION

Variable	<i>r</i>	<i>P</i> (<i>N</i> = 19)
Canopy cover (fifth zone)	0.953	0.0001
Number of large maples	-0.345	0.1486
Number of medium beeches	0.369	0.1195
Maximum canopy cover (second zone)	-0.270	0.2640
Canopy cover (second zone)	-0.377	0.1114
Number of small oaks	0.141	0.5634

than did observations from WS1. A correlation was done between the canonical axis and the six original variables (Table 2). The results from the correlation indicate that the major differences between the two watersheds were that WS4 had more small oaks, more medium birches, and more canopy cover in the fifth vertical zone, while WS1 had more large maples, and more canopy cover and maximum canopy cover in the second vertical zone. These conclusions are possibly erroneous due to the non-significance of most of the correlations. However, the fact that all six variables, except number of small oaks, were univariately significantly different between watersheds lends support to these interpretations.

In view of the differences in vegetation between the two areas, the following hypotheses were formulated and tested.

Hypothesis 1.—The more open canopy in WS4 should allow the birds to maneuver more freely in the air, and could possibly allow birds to detect flying prey more easily. Therefore, birds in WS4 should use more hawks and hovers than birds in WS1. The hypothesis tested was that no difference existed in use of foraging maneuvers between watersheds. The hypothesis could not be rejected ($\chi^2 = 0.526$, *df* = 2, *P* > 0.5, *N* = 231), indicating that birds in both watersheds used each foraging maneuver with similar frequency.

Hypothesis 2.—WS1 has a lower, more dense canopy cover. The trees in WS1, having shorter branches, would have more leaf area per unit branch length. Therefore, birds in WS1 should forage more from leaves and less from branches than birds in WS4. The hypothesis tested was that no difference existed in leaf or branch use between watersheds. The hypothesis could not be rejected ($\chi^2 = 0.020$, *df* = 1, *P* > 0.5, *N* = 162).

Hypothesis 3.—As mentioned before, thickness of vegetation may affect maneuverability of birds. The canopy in WS1 is more compact than that in WS4. Tree crowns in WS1 should be thicker, since natural pruning is

not so advanced in a young forest (Smith 1962). Birds therefore might not move as freely within the tree crowns in WS1, and could therefore forage more efficiently between tree crowns or at the distal branch position. The hypothesis that no difference in use of branch positions existed between watersheds could not be rejected ($\chi^2 = 2.687$, $df = 2$, $P > 0.1$, $N = 162$).

Hypothesis 4.—Results from many studies (e.g., MacArthur and MacArthur 1961, Brewer 1963, James 1971, Whitmore 1977, James 1979) indicate that vegetation structure is probably more important to birds than is the vegetation species composition. Since a difference in tree species composition existed between watersheds, a difference in substrate species-use should also exist. The hypothesis that no difference in substrate species-use existed between watersheds was rejected ($\chi^2 = 32.985$, $df = 6$, $P < 0.005$, $N = 162$). Greater use of oaks and beeches by birds in WS4 comprised the major part of the difference between areas. Whether or not birds used certain tree species groups in excess of the proportion in which the given group occurred could not be tested, because the volume each tree species occupied in the canopy was not known.

Hypothesis 5.—WS4 had less foliage density in the second and third vertical zones than did WS1. Therefore, birds might forage more frequently in the second and third zones in WS4 than in WS1 because the vegetation structure in these zones imposes less physical interference in WS4. The mean foraging height should, therefore, be greater in WS4 than in WS1. The hypothesis that no difference in foraging height existed between watersheds was rejected ($t = 4.578$, $df = 229$, 1-tailed $P < 0.0005$).

The first six foraging variables to enter the stepwise discriminant model were amount of foraging in oak trees, amount of use of the distal part of branches, amount of foraging in beech trees, amount of foraging in birch trees, amount of use of the proximal of branches, and average foraging height. Foraging differed significantly between watersheds ($F_{6,12} = 6.24$, $P = 0.0036$). Birds from WS4 grouped higher on the canonical axis calculated from the coefficients provided by the MANOVA than did birds from WS1. Correlations between the canonical axis and each original variable were calculated (Table 3). The only significant correlation was with amount of oak use. Birds in WS4 foraged more in oaks than did birds in WS1.

One might have predicted that the birds would use different tree species in the two study areas. Oaks, beeches, and birches each occurred in amounts significantly different between watersheds in at least one size class. The amount of small oaks and of medium birches each were among the first six variables to enter the discriminant model on the vegetation variables. However, if vegetation structure is more important than tree species composition, as mentioned under Hypothesis 4, it is possible that

TABLE 3

CORRELATIONS BETWEEN CANONICAL AXIS FOR FORAGING AND THE ORIGINAL VARIABLES, AND PROBABILITY OF GREATER CORRELATION

Variable	<i>r</i>	<i>P</i> (<i>N</i> = 19)
Amount of oak use	0.563	0.0121
Amount of distal branch use	-0.321	0.1796
Amount of beech use	0.429	0.0668
Amount of birch use	0.399	0.0904
Amount of proximal branch use	0.331	0.1659
Mean foraging height	0.449	0.0538

the tree species variables have little biological significance to redstarts. The foraging substrate species may have been determined solely by chance and not by any characteristic of the tree species itself. In view of the above concept, the multivariate analyses on foraging variables were re-done, omitting the tree species variables. In this analysis, the variables which best discriminated between the two groups were average foraging height, amount of hawking, and use of the distal branch position. Foraging differed significantly between watersheds on the basis of these variables ($F_{3,15} = 3.96$, $P = 0.0290$). Birds from WS4 grouped higher on the canonical axis calculated from coefficients provided by the MANOVA. The only significant correlation between the canonical axis and the original variables (Table 4) was with average foraging height.

Several questions were generated in view of the above results. Why did birds use essentially the same maneuvers in both areas? Why did no difference exist in leaf or branch use? Why was use of branch positions univariately nonsignificantly different between watersheds, and multivariately nonsignificantly correlated with the canonical axis?

In an attempt to answer these questions another hypothesis was gen-

TABLE 4

CORRELATIONS BETWEEN CANONICAL AXIS FOR FORAGING (WITH TREE SPECIES VARIABLES OMITTED) AND ORIGINAL VARIABLES, AND PROBABILITY OF A GREATER CORRELATION

Variable	<i>r</i>	<i>P</i> (<i>N</i> = 19)
Amount of hawking	-0.444	0.0568
Amount of distal branch use	-0.421	0.0728
Mean foraging height	0.588	0.0081

erated. Although the vegetation structure differed between areas, perhaps birds foraged in similar habitat in both areas. To test this hypothesis, two new variables were established—canopy cover and percent openings in the vertical zone in which each foraging action occurred. The hypothesis that the mean of each variable was the same in both watersheds was tested using Student's *t*-test. Neither mean canopy cover ($t = 1.216$, $df = 229$, $P > 0.2$) nor mean percent openings ($t = 0.641$, $df = 229$, $P > 0.4$) proved to be significantly different between watersheds. Thus, based on these two variables, the birds seem to have selected similar foraging habitat in both watersheds. Since vegetation in WS1 was more dense than vegetation WS4, birds in WS1 must have picked the more open places in which to forage. The hypothesis that mean percent openings in places of foraging in WS1 did not differ from the overall watershed mean was rejected ($t = 1.876$, $df = 125$, 1-tailed $P < 0.05$). Thus, birds in WS1 seem to have picked the more open places for foraging.

The fact that birds foraged in similar habitat in both watersheds could explain why little difference in foraging behavior between watersheds was observed. In similar habitat density of prey items and time required to pursue prey (Pulliam 1974) should be roughly equal. Thus, the effects of distance between predator and prey (Schoener 1969) would be similar in both watersheds. The physical effect of vegetation structure on bird movement would also be similar.

SUMMARY

The purpose of this study was to determine how vegetation structure affected the foraging behavior of American Redstarts (*Setophaga ruticilla*). Two watersheds in the Fernow Experimental Forest near Parsons, West Virginia were used as study areas. The first area (WS1) is characterized by pole-stage timber. The second area (WS4) is approaching a mature forest.

Ten male redstarts in WS1 and nine male redstarts in WS4 were used in this study. Foraging observations were taken each morning, weather permitting. Later, vegetation was measured in the place in which foraging occurred.

Overall vegetation differed between areas. WS4 had a taller, less dense canopy than did WS1. WS4 contained more oak, beech, and birch trees, while WS1 contained more cherry, maple, and magnolia trees.

Foraging differed between watersheds only in the height of foraging and in the tree species used. Tree species use, however, possibly was not biologically important. The more open canopy in WS4 allowed birds to forage higher.

Vegetation structure in the place of foraging did not differ between watersheds. Birds in WS1 selected places to forage which had more open vegetation than the overall watershed mean.

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LITERATURE CITED

- BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. *Auk* 80:9-49.
- FICKEN, M. S. 1962. Maintenance activities of the American Redstart. *Wilson Bull.* 74: 153-165.
- HOLMES, R. T., T. W. SHERRY, AND S. E. BENNETT. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts. *Oecologia* 36:141-149.
- JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-236.
- AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JAMES, R. D. 1979. The comparative foraging behavior of Yellow-throated and Solitary vireos: the effect of habitat and sympatry. Pp. 137-163 in *The role of insectivorous birds in forest ecosystems* (J. G. Dickson, R. N. Commer, R. R. Fleet, J. C. Kroll, and J. J. Jackson, eds.). Academic Press, New York, New York.
- MACARTHUR, R. H. AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42: 594-598.
- PULLIAM, H. R. 1974. On the theory of optimal diets. *Am. Nat.* 108:59-74.
- SCHOENER, T. W. 1969. Models of optimal size for solitary predators. *Am. Nat.* 103:277-313.
- SMITH, D. M. 1962. *The practice of silviculture*. John Wiley and Sons, Inc., New York, New York.
- TRIMBLE, G. R. 1977. *A history of the Fernow Experimental Forest and the Parsons Timber and Watershed Laboratory*. USDA For. Serv. Gen. Tech. Rept. NE-28. Northeast Forest Experiment Station, Upper Darby, PA.
- WHITMORE, R. C. 1977. Habitat partitioning in a community of passerine birds. *Wilson Bull.* 89:253-265.

DIVISION OF FORESTRY, WEST VIRGINIA UNIV., MORGANTOWN, WEST VIRGINIA 26506. ACCEPTED 1 DEC. 1981.